

Shared drivers but divergent ecological responses: Insights from long-term experiments in savanna grasslands

By: Melinda D. Smith, Alan K. Knapp, Scott L. Collins, Deron E. Burkepile, Kevin P. Kirkman, [Sally E. Koerner](#), Dave I. Thompson, John M. Blair, Catherine E. Burns, Stephanie Eby, Elisabeth J. Forrestel, Richard W.S. Fynn, Navashni Govender, Nicole Hagenah, David L. Hoover, and Kevin R. Wilcox

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Abstract:

Fire and grazing, key determinants of structure and function of savanna grasslands worldwide, have been extensively altered by humans. We used existing long-term manipulations of fire and grazing in North American and South African mesic savanna grasslands, as well as new experiments, to determine whether the impacts of fire and grazing by large herbivores differed between these systems. We found that despite a body of literature suggesting that these savanna grasslands respond uniquely to fire and grazing, their ecosystem responses (aboveground productivity) were generally similar. In contrast, plant-community responses to fire and herbivores diverged strongly between systems. The differences in plant-community responses, as well as convergence in ecosystem function, were underpinned by a common mechanism: the response of grass dominance to changing fire and grazing regimes. As a result, divergent responses of plant communities to altered fire and grazing regimes did not preclude convergence in ecosystem function.

Keywords: aboveground net primary productivity | fire | grassland | grazing | plant community

Article:

The comparative approach in ecology, in which ecological patterns and processes are contrasted between two or more sites, has been a powerful tool for advancing our understanding of ecosystem structure and functioning for decades. From space-for-time studies (e.g., Chapin et al. 1994) and gradient approaches (e.g., Whittaker 1967) to studies of evolutionary convergence

in structure among ecosystems around the world (e.g., Cody and Mooney 1978), as well as the more recent explosion of meta-analyses (e.g., Vetter et al. 2013), ecologists have drawn invaluable insights not possible from single-site studies. Given the global scale of anthropogenic environmental change, there have been increasing calls for comparative, multisite studies capable of determining how and why ecosystems may differ in their responses to global changes (e.g., Fraser et al. 2013). Such interest arises, in part, from a body of research that has linked a common ecosystem change to a wide range of factors. For example, the increase in woody plants observed in grasslands around the world has been attributed to alterations in grazing pressure and fire regimes, as well as increased atmospheric carbon dioxide (CO₂) concentrations and/or climate change (e.g., Briggs et al. 2005, Eldridge et al. 2011). In other cases, very different ecosystem responses can result from changes in the same driver. For example, alterations in the precipitation regimes forecast with climate change can lead to very different ecosystem responses in central US grasslands (e.g., increased productivity in semi-arid ecosystems versus decreased productivity in mesic grassland with more variable precipitation regimes; Heisler-White et al. 2009). Explaining the latter scenario is particularly challenging given that divergent ecosystem responses with alterations in the same driver could be due to inherently different mechanisms causing the response or differences in methodologies that often confound comparisons (Knapp et al. 2004). Multisite comparative experiments, particularly those that are long term, are uniquely suited to address this issue by minimizing confounding methodological differences and revealing the key mechanisms determining ecosystem response (Fraser et al. 2013). This is essential for gaining an improved predictive understanding of ecosystem sensitivity to global environmental change (Smith et al. 2009).

We have employed this comparative approach over the past decade in North American (NA) and South African (SA) savanna grasslands to better understand the consequences of alterations in fire and grazing regimes. Savanna grasslands (*sensu* Scholes and Archer 1997) are structurally similar across the globe (figure 1), and fire and grazing by large herbivores are key determinants of their structure and function (Walker 1985, Archer 1995, Scholes and Archer 1997, Frank et al. 1998, Knapp et al. 1998, Oesterheld et al. 1999, Scholes et al. 2003). A focus on savanna grasslands is relevant given that they cover more than 20% of the terrestrial land surface (Scholes and Archer 1997) and provide critical ecosystem services (Daily et al. 1997). Moreover, these ecosystems are highly imperiled by human activities, which have dramatically altered - herbivore communities and fire and grazing regimes (Archer 1989, Bond et al. 2003). Although savanna grasslands span broad climatic gradients on most continents (Walker 1985, Scholes and Archer 1997, Oesterheld et al. 1999), it is in the mesic portion of the savanna grassland continuum (precipitation more than 500 millimeters MAP in the tropics and more than 600 millimeters MAP outside the tropics; Bond et al. 2003) that fire and grazing are important both separately and interactively (Collins and Wallace 1990, Knapp et al. 1998, Collins et al. 1998). In these regions, fire and grazing regimes are being extensively altered or even eliminated as a result of habitat fragmentation and management practices. These mesic savanna grasslands are the focus of our decade-long investigations.

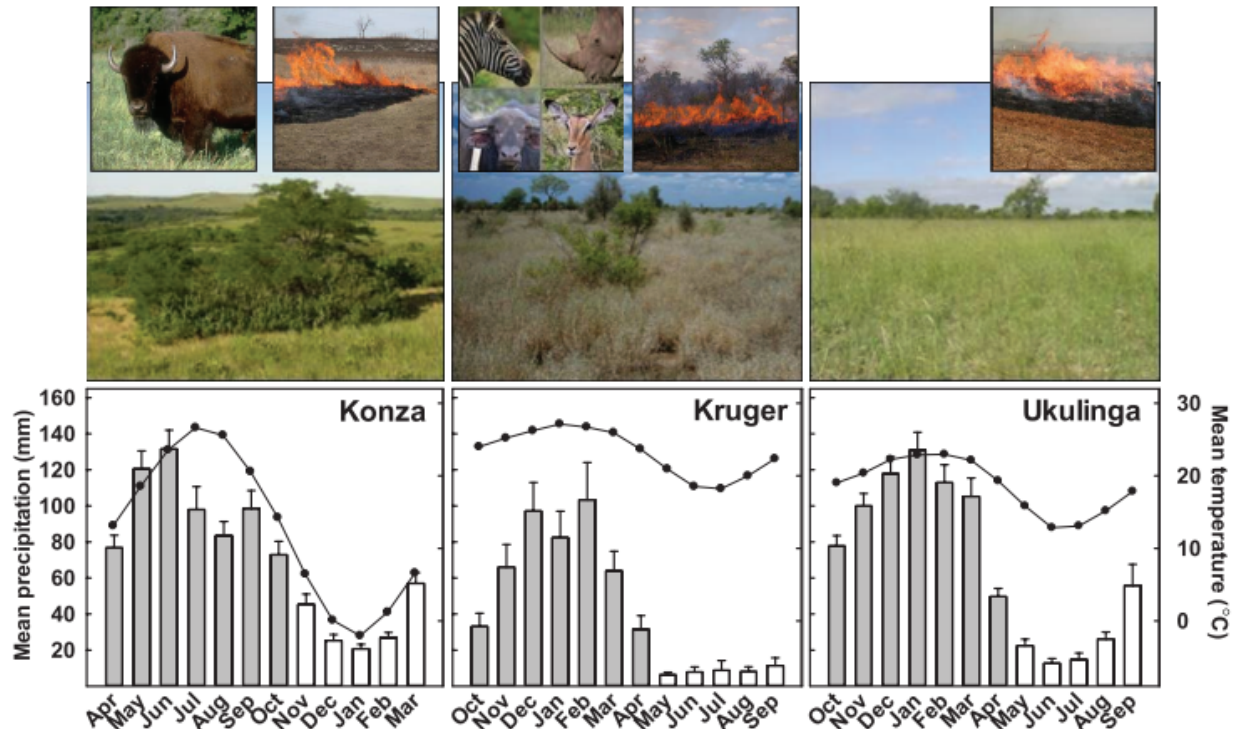


Figure 1. (top) For our study, we focused on three sites with long-term fire-frequency-manipulation experiments with and without native large herbivores present: Konza Prairie Biological Station, Kansas, United States (Konza); Kruger National Park, Mpumalanga, South Africa (Kruger); and Ukulinga Research Farm, KwaZulu-Natal, South Africa (Ukulinga). The savanna grasslands in North America (NA–Konza) and South Africa (SA–Kruger and SA–Ukulinga) are structurally very similar (i.e., both characterized by a continuous grass layer with scattered shrubs and trees) and share common drivers of frequent fire and grazing by large ungulate herbivores. Photographs: Deron Burkpile and Alan Knapp. (bottom) These three sites have similar climates; their growing-season temperatures (in degrees Celsius [°C]) and annual precipitation amounts (in millimeters [mm]) and patterns are comparable, with most precipitation inputs (75%) occurring during the growing season (the gray bars). The primary differences occur in the dormant season, when temperature and the environmental cues that start spring growth differ (i.e., temperature in NA versus rainfall in SA), as is expected in temperate versus subtropical systems. Shown are the long-term (20 or more years) patterns of air temperature (the lines) and precipitation (the bars) for the Konza, Kruger, and Ukulinga study sites. Adapted with permission from Buis and colleagues (2009).

Given these similarities and the strong consensus of the importance of fire and grazing in these systems (Collins and Wallace 1990, Frank et al. 1998, du Toit et al. 2003, Bond et al. 2003), one expectation is that savanna grasslands should respond similarly to fire suppression or the loss of large herbivores. However, syntheses of numerous site-based studies (Booyesen and Tainton 1984, Collins and Wallace 1990, Scholes and Walker 1993, Knapp et al. 1998, Frank et al. 1998, Milchunas et al. 1988, McNaughton 1985, du Toit et al. 2003) suggest that alterations in these key determinants can have divergent impacts on savanna grasslands across the globe. These include reported differences in the responses of primary production and soil N to fire (Knapp and Seastedt 1986, Blair 1997 in NA versus Tainton et al. 1978, Morris and Fynn 2001 in SA) and a remarkable divergence in responses of plant-community structure and dynamics to both fire and grazing (Collins and Glenn 1991, Hartnett et al. 1996, Collins et al. 1998 in NA versus Morris et al. 1992, Morris and Tainton 1996, Titshall et al. 2000, Fynn et al. 2004, Uys et al. 2004 in SA). Therefore, savanna grassland responses to alterations in fire and grazing appear to be system specific and potentially contingent on a number of factors, including

differences in evolutionary history, ecosystem age, and the extant large herbivore assemblages (table 1).

Table 1. The similarities and differences in attributes and responses of North American (NA) and southern African (SA) savanna grasslands.

Common ecological attributes or responses		Different ecological attributes		
			NA	SA
Climate	Climate variation key driver, Precipitation limits ANPP	Age of biome (yrs)	5 million–6 million	40 million–60 million
Frequent fire	Reduces woody plants, Increases N limitation	Age of community (years)	8,000–10,000	4 million–6 million
Grazing	Controls plant diversity, Grazers favor burned sites	Climate	Temperate	Subtropical
N limitation	N addition shifts plant species composition and increases ANPP	Dormant season	Winter (cold)	Winter (dry)
Plant community	Dominated by C ₄ grasses with abundant trees/shrubs	Soil nutrients	High	Low
		Current herbivore richness	Low	High
		C ₄ grass diversity	Low	High

Note: It is the differences in attributes that are thought to underlie disparate plant-community and ecosystem responses to fire and grazing between NA and SA. Adapted with permission from Koerner and Collins (2013).

It is important to consider, however, that these site-based studies were conducted independently, often with methods and approaches that differed considerably (Knapp et al. 2004). As a consequence, direct comparisons may be limited in their ability to detect common responses, particularly for ecological attributes that are strongly scale and sampling dependent (e.g., diversity; Scheiner et al. 2000). In fact, these types of comparisons may be prone to identifying differences in responses but for the wrong reasons: due to different methodologies rather than system differences. An additional problem is that studies of savanna grasslands are biased geographically. The Northern Hemisphere has been more extensively studied—at least in terms of papers published—than the Southern, and many of the most comprehensive studies have been in the United States (e.g., Archer et al. 1988, Knapp et al. 1998, Tilman et al. 2001, Scholes et al. 2003). Some notable exceptions include east African savanna grasslands, where grazing by large herbivores, but not fire, has been investigated intensively (e.g., McNaughton 1985, Anderson et al. 2007, Young et al. 2013, Keesing and Truman 2014).

This raises important questions about our understanding of savanna grasslands as a globally important biome: Is our knowledge of fire and grazing by large herbivores sufficiently general to enable us to forecast how ecosystem structure and function will respond as fire and grazing regimes change? Have the different methods and approaches used in the study of these systems led to perceived differences in the role of fire and grazing? Or are the impacts of the shared drivers on ecological processes truly different in systems with, for example, different evolutionary histories and large herbivore assemblages (e.g., NA versus SA; table 1)? To address these questions, we conducted explicitly comparative studies within existing long-term (more than 25 years) experiments, as well as initiated new long-term experiments, in representative mesic savanna grassland sites in NA and SA. Although large herbivore assemblages can be manipulated, evolutionary history is impossible to manipulate as an ultimate causal factor. However, well-designed comparative studies are powerful in distinguishing between

evolutionary versus ecological mechanisms (Losos 1996). Such designs require that ecological variables be measured in the same way on different continents, as well as across habitats or treatments within each continent (Schluter and Ricklefs 1993). Our overarching goals with this comparative research were to (a) identify whether plant-community and ecosystem responses to alterations in fire and grazing were similar or different between mesic savanna grasslands in NA and SA and (b) assess whether and how mechanisms determining plant-community and ecosystem responses to altered fire and grazing regimes differed between the study systems.

Comparative experimental approach

Central to our comparative research was the establishment of identical experiments in climatically and structurally similar savanna grasslands in NA and SA where extant native large herbivore assemblages were either present or absent (figure 1). Our specific objectives were to assess the following: (a) the effects of long-term (more than 30 years) alterations in fire regimes in the absence of native large herbivore grazing, (b) the effects of long-term alterations in fire regimes (more than 25 to 50 years) in the presence of native large herbivore grazing, (c) the impacts of the loss of native large herbivores (more than 5 kilograms) on key ecosystem processes and plant-community structure and dynamics, and (d) how alterations in fire regimes may modify the impacts of loss of large herbivores. We focused our studies on the herbaceous component of the plant community rather than on the more frequently studied woody component, because from a structural perspective, responses to fire and grazing are thought to differ much less for the woody than for the herbaceous portion of the plant community (Titshall et al. 2000, Bond et al. 2003, Higgins et al. 2007).

For almost a decade, we collected data using identical sampling protocols on key plant-community (richness, diversity, composition) and ecosystem (aboveground productivity, soil N availability) responses, as well as data capturing potentially important mechanisms of change (large herbivore abundance and distributions, plant traits). This allowed us to directly compare measured responses between the study sites in order to determine whether plant-community and ecosystem responses to alterations in fire and grazing regimes differed without the confounding influence of differences in methodologies.

To address the long-term effects of alterations in fire regimes in the absence of large herbivores, we used existing long-term experiments at the Konza Prairie Biological Station in NA (Konza) and at the Ukulinga Research Farm in SA (Ukulinga), in which fire frequency (burned every year, every 3–4 years, or unburned) had been manipulated for more than 30 years in sites lacking large herbivores (figure 1). In addition, because frequent burning over the long term can result in nitrogen limitation with consequent effects on ecosystem processes (Blair 1997, Collins et al. 1998), we conducted identical N-addition experiments at Konza and Ukulinga to determine whether this potential mechanism underlying the ANPP fire response was common to both sites.

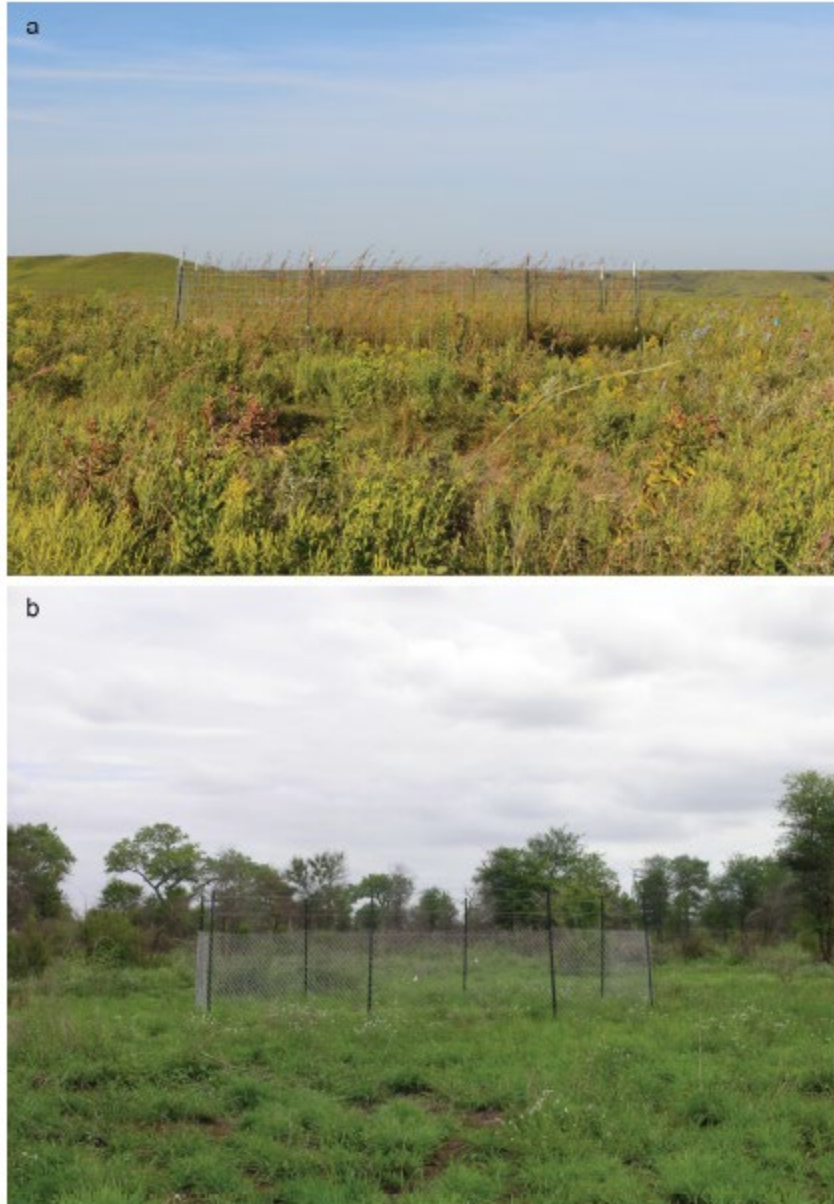


Figure 2. Examples of the permanent large herbivore exclosures (7 meters [m] in diameter \times 2.2 m tall; 38.5 square meters [m²]) established at Konza (a) and Kruger (b). The Konza study site is dominated by rhizomatous (sod-forming) C₄ grasses, such as *Andropogon gerardii* and *Bouteloua gracilis*, whereas the Kruger study site is dominated by caespitose C₄ grasses, such as *Bothriochloa radicans* and *Themeda triandra* (see figure 8). Shown here are sites burned annually (Konza) and every 3–4 years (Kruger). Each exclosure consists of fencing to a height of 1.8 m and two strands of wire located above the fencing to a height of 2.2 m. This design effectively excludes all large herbivore species (more than 5 kilograms). Photographs: Catherine Burns and Melinda Smith.

To assess interactions between long-term alterations in fire regimes and grazing by large herbivores, we again used a long-term (more than 25 years) experiment at Konza in which fire frequency had been manipulated, but in this case, the native large herbivore, bison (*Bos bison*), was present (figure 1). We also took advantage of a long-term (more than 50 years) fire-frequency-manipulation experiment at the Kruger National Park in SA (Kruger), where a diversity of large herbivores (12 species; Burkepile et al. 2013) was present. Within these long-

term experiments, we constructed permanent exclosures in sites burned every year (annually), burned every 3–4 years (intermediate), or left unburned (figure 2). This allowed us to examine how the loss of large herbivores affects both sites in directly comparable ways. It is important to emphasize that before this study, the independent and interactive effects of fire and grazing had not been experimentally assessed in SA, despite intensive study of these in NA (Collins and Wallace 1990, Knapp et al. 1998). Typically, effects of herbivory in SA (and other areas of Africa) are studied in exclosures with fire excluded or with a variable fire regime (McNaughton 1985, Young TP et al. 1998, 2013, Jacobs and Naiman 2008). Alternatively, fire is often manipulated without controlling for herbivory (Tainton et al. 1978, Morris and Fynn 2001, but see Augustine and McNaughton 2006). Therefore, rigorous comparisons of SA systems with NA systems were not possible prior to our study.

Finally, given the differences in large herbivore diversity between NA and SA (table 1) and the potential for this to strongly influence responses to herbivore exclusion, we established exclosures in an existing approximately 900-hectare enclosure at Kruger that was originally built with the goal of breeding tuberculosis-free African buffalo (*Syncerus caffer*). This allowed us to compare the effects of a single, functionally similar large herbivore species at both sites—bison at Konza versus African buffalo at Kruger (both true grazers, sensu du Toit et al. 2003).

Responses to alterations in fire and grazing

In general, our expectation was that fire and grazing would be qualitatively similar in their effects on ecosystem processes, such as aboveground net primary productivity (ANPP). However, we predicted that the magnitude of the responses would differ because of broad differences in soil fertility between NA and SA (table 1), with responses more constrained in SA because of greater N limitation. In contrast, we expected system-specific effects (both in magnitude and direction) of fire and grazing on plant-community responses as a consequence of differences in diversity of large herbivores and traits and diversity of C₄ grasses between the systems (table 1).

The conceptual basis for differences in plant-community responses versus similarities in ecosystem responses is founded in the ways in which evolutionary history and the resultant assemblage of plant species and traits are manifest at these two hierarchical levels. C₄ grasses are the most abundant herbaceous species in both NA and SA savanna grasslands, and as a consequence, these dominant species contribute most to ecosystem function and community structure. In both NA and SA, changes in abundance of C₄ grasses can have important consequences for plant-community diversity, species turnover, and species interactions in response to fire and grazing (McNaughton 1985, Milchunas et al. 1988, Collins et al. 1998, Collins and Smith 2006). A longer evolutionary history with these drivers in SA has allowed for extensive diversification of C₄ grasses (Scholes et al. 2003). By contrast, only a few broadly distributed C₄ grasses dominate the younger communities in NA. We expected that these differences in the diversity and evolutionary history of the dominant C₄ grasses would lead to divergent plant-community responses to fire and grazing in NA and SA.

In addition, differences in large herbivore diversity between NA and SA are likely to be important. Bison in NA often preferentially consume C₄ grasses, reducing their competitive

impacts and increasing species diversity. Indeed, diversity declines when bison are absent (Collins et al. 1998, Koerner et al. 2014). Plant-community structure and dynamics may respond differently to grazing in SA because the diverse array of large herbivores will consume both grasses and forbs regardless of fire regime (Kartintzel et al. 2015). For example, when herbivores are present, grazers (e.g., rhinoceros, zebra, wildebeest, impala) will consume C₄ grasses reducing their competitive impacts, much like in NA, but browsers (e.g., greater kudu, impala, steenbok) will also consume forbs, potentially suppressing species diversity. When herbivores are removed, grasses would likely become competitive dominants with the removal of grazers and outcompete forbs that colonize following the removal of browsers. These combined effects could result in a lesser and/or delayed change in plant diversity with the removal of herbivores, in contrast to the responses in NA. However, because C₄ grasses are always dominant in the herbaceous community on both continents and likely share similar functional traits (e.g., C uptake, water use efficiency, N requirements, litter quality), the responses of ecosystem processes to fire and grazing should be similar.

Below, we show that a decade of comparative research between NA and SA has revealed that some responses are indeed generalizable, whereas others are more system specific and contingent on factors, such as differences in plant species traits and their phylogenetic histories, as well as diversity of large herbivore assemblages. However, despite these differences, there are common mechanisms between the two systems that underpin their responses. This suggests that generality may be best achieved by understanding how common mechanisms operate in different systems.

Effects of fire in the absence of grazing

In the absence of large grazers, the effects of altered fire regime on ANPP in savanna grasslands can be substantial (Knapp et al. 1998, Kirkman et al. 2014). Research conducted in NA savanna grasslands, now spanning more than half a century, has consistently shown ANPP to be greater in years with fire, especially dormant-season or early-spring fire (e.g., Knapp et al. 1998, Oesterheld et al. 1999). The mechanisms responsible for this are numerous and include those that suppress ANPP in sites without fire (litter accumulation), to those that stimulate ANPP in the post-fire environment (increased light availability), to shifts in plant-community composition with increased dominance by highly productive C₄ grass species (Knapp and Seastedt 1986, Blair 1997, Knapp et al. 1998). There has been much less focus on fire effects in the absence of large herbivores in savanna grasslands of SA (Scholes et al. 2003).

We now have evidence that ANPP responses to alterations in fire are consistent at Konza and Ukulinga (figure 3, top). ANPP was always lowest in unburned sites at both Konza and Ukulinga, and when fire occurred, ANPP increased significantly (figure 3, top). Similarly, soil depth and soil water availability affected ANPP responses to fire consistently at both sites—with ANPP 30%–90% higher in annually burned treatments in sites with deep soils but no effect of fire in those with shallow soils (Buis et al. 2009).

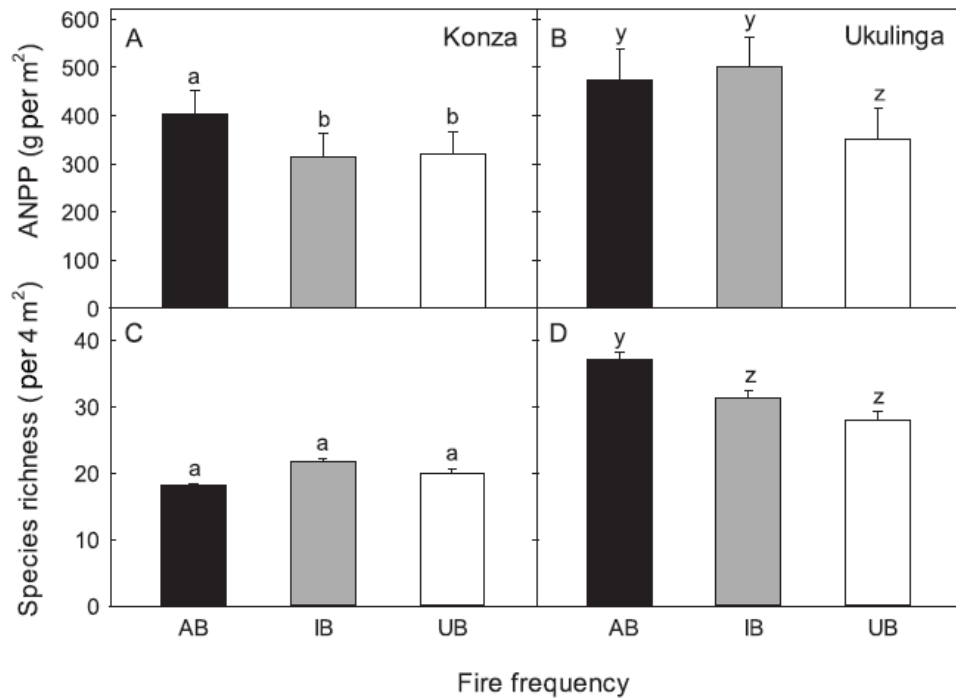


Figure 3. (top) Aboveground net primary productivity (ANPP, in grams [g] per square meter [m²]) responds similarly to long-term (more than 30 years) alterations in fire regimes in the absence of large herbivores in North American (Konza) and South African (Ukulinga) savanna grasslands. ANPP was consistently highest with annual burning but lowest in the absence of fire. Adapted with permission from Buis and colleagues (2009) with three additional years of data. (bottom) In contrast, plant species richness (per 4 m²) responds differently to long-term alterations in fire regimes without large herbivores between Konza and Ukulinga. For Konza, fire has no significant effect on plant species richness (although richness tends to peak at intermediate fire frequency), whereas richness is highest with annual burning and lowest in the absence of burning at Ukulinga. Modified from Kirkman and colleagues (2014). Both ANPP and richness are means from 2005–2010. The different letters denote significant differences ($\alpha < .05$) between fire-frequency treatments. Abbreviations: AB, annually burned (black bars); IB, intermediate fire frequency (burned every 3–4 years; gray bars); UB, unburned (white bars).

Frequent fire can also affect plant-community richness, primarily through a reduction in forb richness in savanna grasslands of NA (Collins et al. 1998, Collins and Calabrese 2012), but results from other systems have been equivocal (e.g., Uys et al. 2004). We found strong differences in the response of total plant species richness to fire frequency between Konza and Ukulinga (figure 3, bottom). Consistent with other studies at Konza (Collins and Calabrese 2012), we found similar levels of total richness in annually, intermediate and unburned grasslands, although richness tended to be lower in annually burned sites and higher in sites burned every 4 years (figure 3, bottom). The trend at Konza reflects a decrease in forb richness under high fire frequency (Kirkman et al. 2014). In contrast, species richness was highest with annual burning and lowest in the absence of fire at Ukulinga. The increase in richness at Ukulinga under annual burning occurred because of a combined increase in both forb and grass species (Kirkman et al. 2014). Therefore, plant-community responses to frequent fire were divergent, despite consistent responses in ANPP.

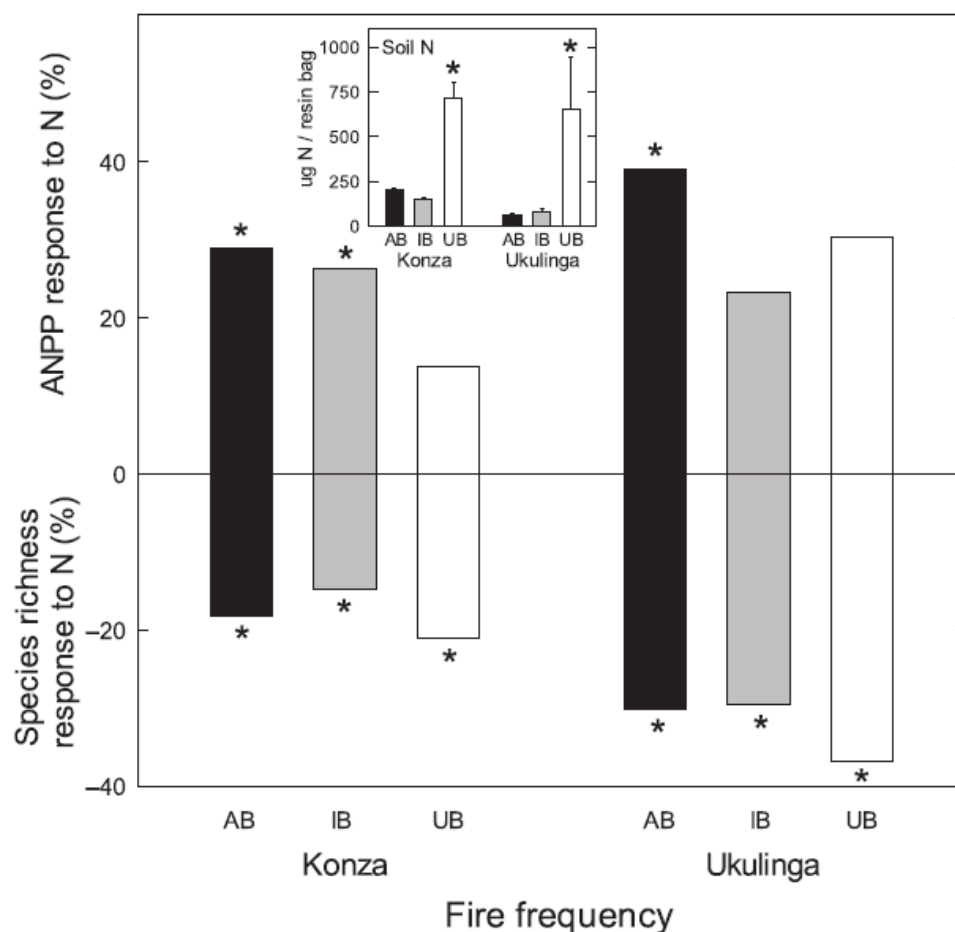


Figure 4. (top) Aboveground net primary productivity (ANPP, in grams [g] per square meter [m^2]) increases significantly with nitrogen (N) addition (10 g per m^2) in both North American (Konza) and South African (Ukulinga) savanna grasslands. ANPP response, expressed as the percentage difference between N addition and control plots, was consistently greatest with annual burning at Konza and Ukulinga. Shown are the data from 2010 after 5 years of N addition. (bottom) Plant species richness decreases with N addition for Konza and Ukulinga. The response of plant species richness (per 4 per m^2) to N addition is expressed as the percentage difference between N-addition and control plots. This response was significant irrespective of burn treatment at both sites. The asterisks denote significant ($\alpha < .05$) differences in ANPP or plant species richness between the N addition and control plots. Adapted with permission from Kirkman and colleagues (2014). Abbreviations: AB, annually burned (black bars); IB, intermediate fire frequency (burned every 3–4 years; gray bars); UB, unburned (white bars). (inset) Frequent fire consistently decreases soil N availability (micrograms [mg] N per resin bag) at Konza and Ukulinga when compared with the unburned treatment. The asterisks denote significant ($\alpha < .05$) differences in soil N availability between the fire-frequency treatments, with UB being significantly different from the AB and IB treatments at both sites. Adapted with permission from Buis and colleagues (2009).

Although aboveground productivity increases with frequent fire in the absence of grazing at Konza, a number of studies have shown that N limitation to plant growth is greater in frequently burned sites compared with that in unburned sites (Seastedt et al. 1991, Blair 1997). We found similar responses in the long-term fire treatments at Ukulinga with several-fold lower levels of extractable inorganic N in soils of annually burned treatments compared with those of the unburned treatments (figure 4, inset). The addition of N to plots also revealed comparable patterns of N limitation with ANPP significantly increased (approximately 25%–35%) in annually burned treatments, and no ANPP response to N addition in unburned treatments at both Konza and Ukulinga (figure 4, top).

Increased nitrogen availability also decreases species richness in mesic herbaceous communities (e.g., Gough et al. 2000). Unlike the dissimilar richness response with fire frequency, species richness declined at both Konza and Ukulinga with N addition (figure 4, bottom). The decline in richness was consistent within sites across fire frequencies, but the response was stronger at Ukulinga (an approximately 18% decline on average at Konza, a more than 30% decline at Ukulinga), which has a larger plant species pool and potentially stronger N limitation in burned treatments than at Konza (figure 4, inset; Kirkman et al. 2014). Therefore, although the richness response to fire differed between sites, the richness response to increased N availability was consistent across these sites.

The combined effects of fire and grazing

From the plant's perspective, herbivory has traditionally been viewed as a negative interaction. However, studies in savanna grasslands suggest that individual plants, as well as primary productivity at the ecosystem scale, may respond in a neutral (complete compensation) or even a positive manner (overcompensation) to grazing (Frank et al. 1998, McNaughton 1985). We compared ANPP in actively grazed areas with ANPP within grazing exclosures in both Konza and Kruger and found no significant differences regardless of fire regime (Knapp et al. 2012). Therefore, we now have evidence for consistent compensation of ANPP to the combined effects of fire and grazing at both Konza and Kruger.

Native large herbivores in NA savanna grasslands strongly influence plant-community structure and dynamics because the primary herbivore, bison, consumes the dominant C₄ grasses, reducing their abundance and leading to large changes in composition (Collins et al. 1998, Knapp et al. 1999). The diverse forb flora, in turn, responds positively thereby increasing herbaceous plant diversity and altering composition (Hartnett et al. 1996, Collins et al. 1998, Collins and Smith 2006). Moreover, grazing promotes diversity irrespective of the frequency of fire (Collins et al. 1998). However, given that herbivores are attracted to recently burned sites (Briggs et al. 1998, Fuhlendorf and Engle 2001), the increase in diversity may be greatest for burned sites when compared with unburned sites. In contrast to this NA response, herbaceous plant-community diversity in SA may respond similarly across all fire regimes. This is because the more diverse herbivore assemblage can both reduce the dominance of C₄ grasses via grazers—such as zebra (*Equus quagga*), wildebeest (*Connochaetes taurinus*), and African buffalo—and reduce the less abundant forbs by mixed feeders, such as impala (*Aepyceros melampus*), and browsers, such as kudu (*Tragelaphus strepsiceros*; du Toit et al. 2003, Jacobs and Naiman 2008). However, a similar response to the NA site may be expected with a single, functionally similar herbivore species in SA (i.e., bison in NA versus African buffalo in SA).

We found that plant richness in grazed sites was highest with intermediate burning at Konza (figure 5a), similar to the trend observed in the absence of grazing over the long term (figure 3, bottom) except that total richness was twofold higher under grazing. An increase in forb richness primarily drove this twofold higher richness (Eby et al. 2014). Therefore, grazing can increase diversity overall by allowing more forb species to persist. In contrast, richness was highest in the absence of burning at Kruger, irrespective of whether a single (African buffalo) or multiple herbivore species were present (figure 5b and 5c). This suggests that the single-grazer and

multiple-herbivore assemblages have similar negative impacts on plant richness with frequent fire. Therefore, plant-community responses to fire in grazed grasslands were divergent, despite evidence for consistent compensation in ANPP across fire frequencies.

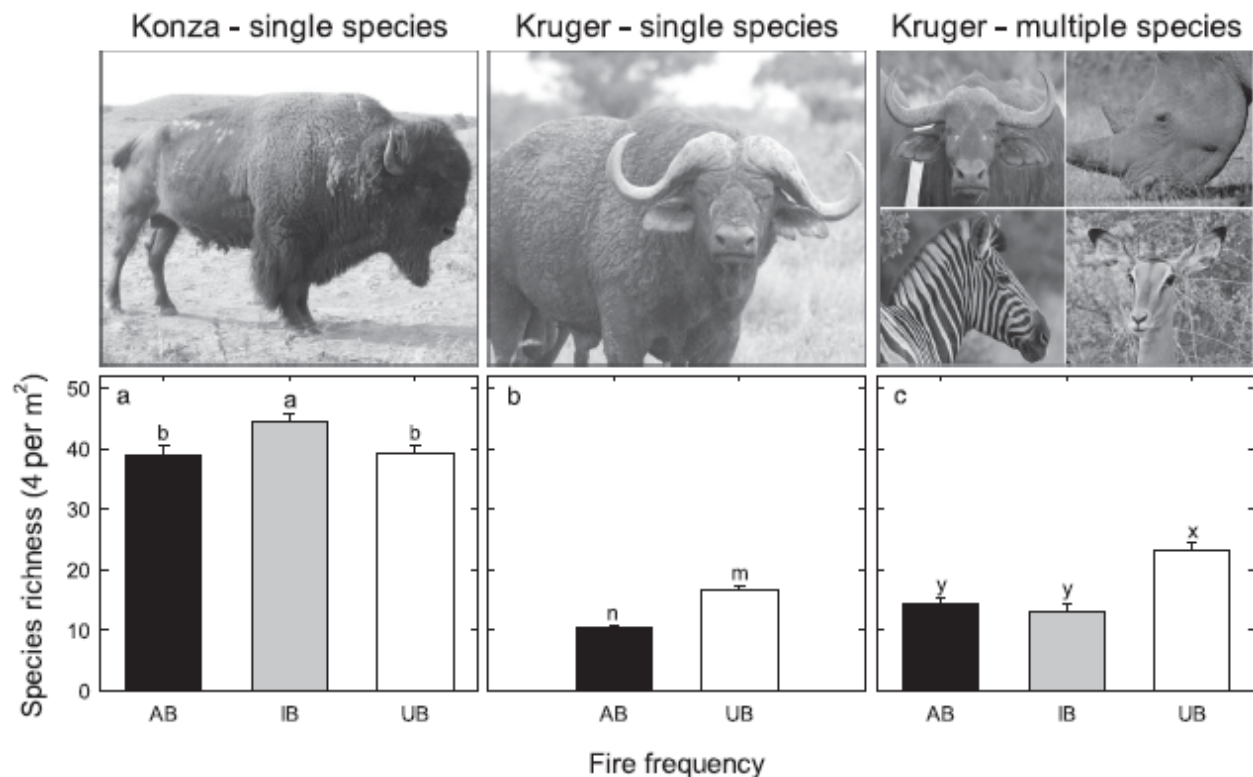


Figure 5. (top) Large herbivores at each of the three study sites in NA (Konza) and SA (Kruger). (bottom) The effects of long-term (25 years at Konza, more than 50 years at Kruger) alterations in fire frequency (annual burn, AB; intermediate burn, 3- to 4-year return interval, I; or unburned, UB) in the presence of large herbivores (control plots) on total plant species richness in 2006. (a) At Konza, richness is highest at an intermediate burn frequency when combined with bison grazing. (b and c) At Kruger, richness was highest in the absence of burning when either a single grazer was present (African buffalo, *Syncerus caffer*) or when multiple herbivores were present. Mean richness is measured at the 4-per-m² plot level. The error bars represent the standard error. Significant differences ($\alpha < .05$) between fire treatments within a site are represented by different letters. Adapted with permission from Koerner and colleagues (2014) and Eby and colleagues (2014). Photographs: Deron Burkepile and Alan Knapp.

Herbivore loss and uncoupling the effects of fire and grazing

As we stated above, ANPP is expected to be greatest with frequent burning in the absence of grazing by the single grazer species in NA because of decreased light limitation and the increased abundance of the dominant C₄ grasses, which appear to be superior competitors with fire-induced decreases in soil N availability (Blair 1997, Knapp et al. 1998). We predicted a similar response in SA with the exclusion of both a single large herbivore, African buffalo, which is functionally similar to bison in NA (i.e., a true grazer *sensu* du Toit et al. 2003), and multiple large herbivore species, as long as true grazers (e.g., zebra, African buffalo; du Toit et al. 2003) were present in the community. After almost a decade of large herbivore exclusion at Konza, the ANPP response to burning has been inconsistent (figure 6a), with no overall difference in ANPP between burned and unburned sites over time. Similarly, no consistent effect of fire on ANPP was observed with either the loss of a single grazer or multiple herbivores in

Kruger (figure 6b and 6c). However, at both NA and SA sites that have not experienced grazing for more than 30 years, we showed that ANPP increases with frequent burning (figure 3). Therefore, the effects of the loss of large herbivores on ANPP appear to develop slowly. Testing this expectation will require longer-term studies to capture this protracted ecosystem response.

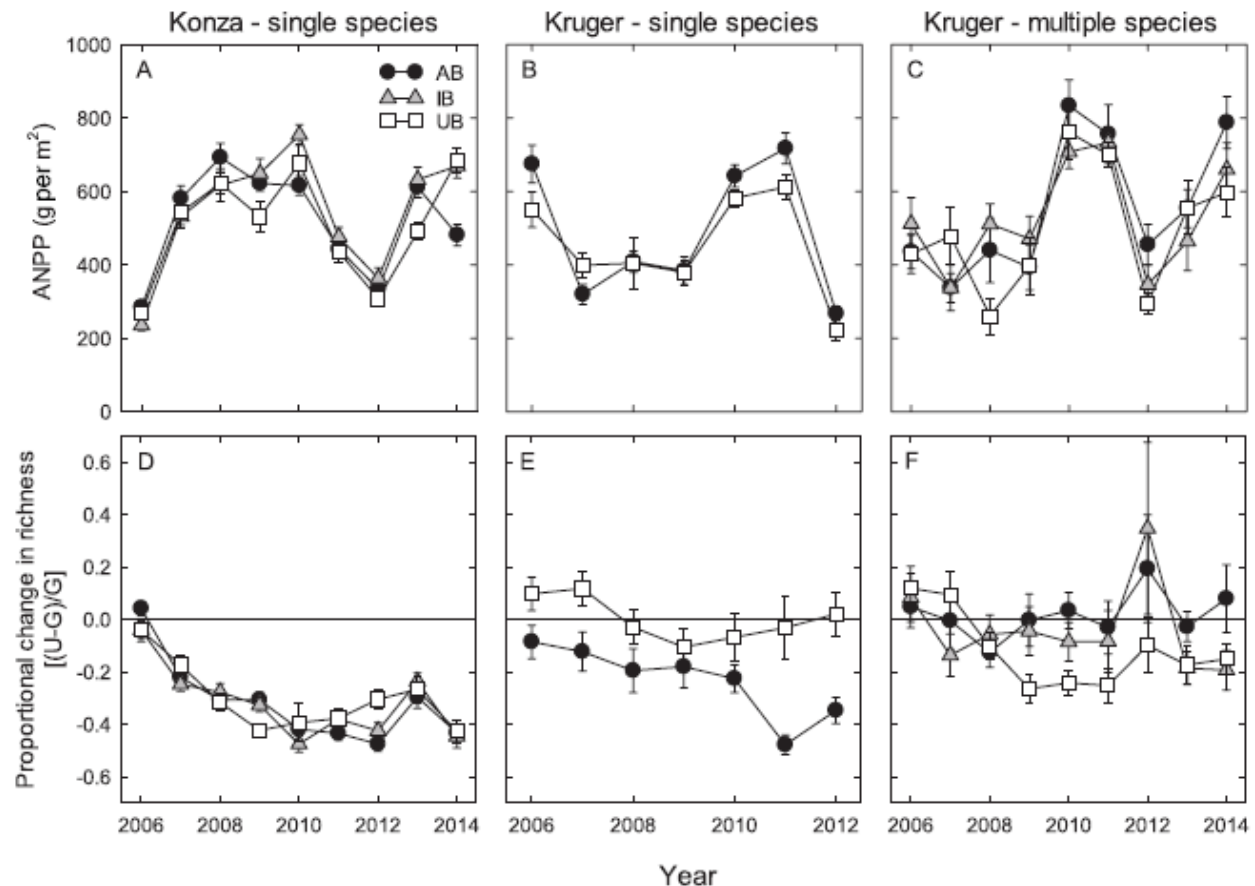


Figure 6. A comparison of Konza and Kruger with a single large herbivore species (left, middle panels) and Kruger with multiple herbivores (right panels) under different fire frequencies (AB, annual burn, black circles; IB, intermediate burn, gray triangles; UB, unburned, white squares). (top) Total aboveground net primary production (ANPP, in grams [g] per square meter [m²]) response to fire frequency in these savanna grasslands has yet to show consistent trends after nearly a decade of herbivore exclusion. ANPP was measured in three 0.01-m² quadrats inside each exclosure and averaged to obtain one measure per exclosure. Each point represents the average across exclosures, and the error bars represent the standard error. (bottom) The proportional effect of herbivore loss on plant richness under three different burn frequencies. Richness at the 4-per-m² plot level was measured in grazed and ungrazed plots. The proportional change in richness was calculated as (ungrazed–grazed)/grazed. A proportional change below zero means that the removal of herbivores decreased richness. Modified from Koerner and colleagues (2014) and Eby and colleagues (2014) with two additional years of data.

In savanna grasslands, herbivores tend to increase plant-community diversity by altering plant-community structure (Collins 1987, Hartnett et al. 1996) through selective grazing of the dominant grasses. In observational studies, we found that long-term ungrazed sites had the lowest richness and diversity at both Konza and Kruger compared with sites with a single grazer species regardless of burn frequencies (Burns et al. 2009, Koerner and Collins 2013). Therefore, we hypothesized that the experimental removal of bison from Konza and African buffalo from Kruger would result in a large decrease in plant-community richness and shift community

composition toward greater dominance by C₄ grasses and that this effect would be most pronounced with annual burning. However, we expected that removal of the much more diverse suite of large herbivores at Kruger also would result in minimal changes in richness and composition because of the combined effects of grazers targeting grasses and browsers targeting forbs.

Through 9 years of large herbivore exclusion, richness strongly and rapidly declined (figure 6d), and community composition changed dramatically at Konza across all fire regimes (Koerner et al. 2014). In Kruger, when only a single grazer species was present, there was a strong decrease in species richness and shift in composition with grazer removal in annually burned areas, similar to the response observed at Konza (figure 6e; Eby et al. 2014), but no consistent change in richness occurred in unburned areas. When the diverse large herbivore community was excluded, there was no consistent change in plant species richness with annual burning (figure 6f). However, for the intermediate and unburned areas, plant richness did decline but at a slower rate and to a lesser extent than with a single grazer either at Kruger or Konza (figure 6f; Koerner et al. 2014). Therefore, as we predicted, plant-community responses to large herbivore loss (single versus diverse suite of herbivores) were divergent, both in the magnitude of change and how responses were modified by fire. This suggests that herbivore diversity plays an important role in determining divergent responses to fire and grazing in NA versus SA.

Evidence for both convergent and divergent responses to fire and grazing

The strongest evidence for convergence in ecosystem responses between the two systems was with the effects of long-term alterations in fire frequency in the absence of grazing. In this case, frequent fire increased ANPP in both NA and SA, and the combination of frequent fire and nitrogen addition further increased productivity, suggesting that frequent burning leads to nitrogen limitation of ANPP in both systems. In contrast to this example of convergence, divergence in plant-community responses was consistently observed with long-term alterations in fire both with and without grazing.

At the outset, we expected that similar ecosystem responses between NA and SA savanna grasslands would result from convergence in functional traits and responses of the C₄ grasses that dominate the herbaceous community on both continents. We have evidence to suggest that this is an important mechanism underlying the increase in ANPP observed with long-term alterations in fire frequency in the absence of grazing. We found that for the NA and SA systems, even though the species and phylogenetic diversity of C₄ grasses differed considerably, the functional and phylogenetic responses to fire were similar. This was because the Andropogoneae species that increased in abundance with frequent fire at both sites are capable of rapid growth in a high-light, low-nitrogen environments (Forrestel et al. 2014). Therefore, although the evolutionary histories of the two savanna grasslands differ, the mechanisms underlying the ANPP response to fire in the absence of grazing are very similar—increased abundance of Andropogoneae species—leading to functionally similar responses between the two systems. We expect that these functional similarities may lead to convergence in ANPP response to loss of grazing, but because of differences in other traits (see below), convergence in responses may not be realized for some time because it may require significant plant compositional change to occur.

In contrast, we expected differences in plant-community responses to alterations in fire and grazing to result from differences in the diversity and evolutionary history of the dominant C₄ grasses, as well as differences in large herbivore diversity between NA and SA. Our findings suggest that both of these mechanisms are important. However, although differences in large herbivore diversity between NA and SA savanna grasslands appear to be a contributing factor to the divergent plant-community responses to the loss of large herbivores, when we compared plant-community responses to the loss of a single, functionally similar grazer species, the direction of response was consistent at both sites, albeit weaker at Kruger. Furthermore, when only grazers (e.g., zebra, wildebeest, African buffalo) were excluded at Kruger, responses were similar to those with complete herbivore exclusion. Therefore, even controlling for the diversity of large herbivores, it appears that differences in the responses and diversity (species, trait, and phylogenetic) of C₄ grasses is crucial for explaining the divergence in plant-community responses to alterations in fire and grazing between NA and SA. Below we address how differences in large herbivore diversity and diversity of C₄ grasses appear to drive the divergent community responses between the two study systems.

The role of large herbivore diversity

Fire affects multiple aspects of savanna grasslands, such as plant-nutrient content, the abundance of palatable grasses, and the density of woody vegetation, that often influence how herbivores select for different habitats (Archibald and Bond 2004, Burkepile et al. 2013). The selection among different fire regimes by different herbivores may be a driver of divergent patterns in the response of plant species richness to grazing exclusion across Konza and Kruger. At Konza, bison appear to have a very broad distribution with preferences for the different burn treatments varying among years but with little consistent selection for any fire frequency (figure 7). Although bison often select annually burned sites early in the growing season to capitalize on the flush of new grass tissue, our data show that they use all burn types relatively equally when averaged across the growing season. Therefore, their impact on plant communities appeared to be relatively even and consistent across burn regimes (figure 7). This pattern of use is likely driven by the fact that the dominant, palatable grass, *Andropogon gerardii*, is in relatively high abundance in grazed areas irrespective of fire regime (figure 8).

However, patterns in herbivore selectivity appear more dynamic in Kruger, with the three most common herbivore species having different preferences for different fire treatments (figure 7). For example, wildebeest and zebra had very different selectivity patterns, with wildebeest strongly preferring annual burns and zebra having more diverse habitat preferences and often using all burns at some level (figure 7). Impala, by far the most abundant herbivores at the study site, exhibited still different patterns in selectivity, often preferring the unburned areas and selecting against annually and triennially burned areas. Therefore, one of the reasons that there may have been less of an impact of herbivores on plant-community composition in Kruger is that the diverse suite of herbivores in Kruger had wide ranges in their preferred habitats, which may have resulted in very different top-down impacts on the herbaceous plant communities. This contrasts with the very consistent impact of bison across all fire regimes in Konza. Indeed, the strongest impacts of herbivore loss on the plant community in Kruger were in unburned areas, which were often selected for by impala, the most abundant herbivore in the system.

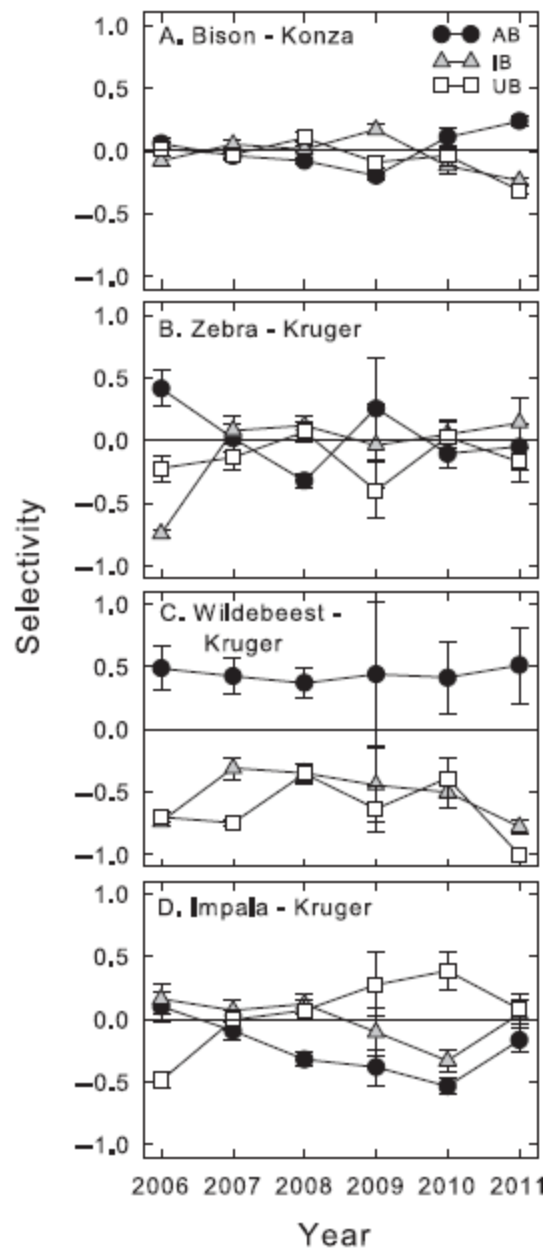


Figure 7. Ivlev's selectivity calculations based on diurnal visual surveys for bison (a) at Konza and the most abundant herbivores at Kruger—zebra (b), wildebeest (c), and impala (d)—for different fire-frequency treatments (AB, annual burn, black circles; IB, intermediate burn, gray triangles; UB, unburned, white squares) across sampling years. Data are means and 95% confidence intervals. The positive numbers denote selection for a fire-frequency treatment, whereas negative numbers denote avoidance. Selectivity 95% confidence intervals that cross the zero line were not considered significant. Adapted with permission from Burkepile and colleagues (2013) with an additional three years of data.

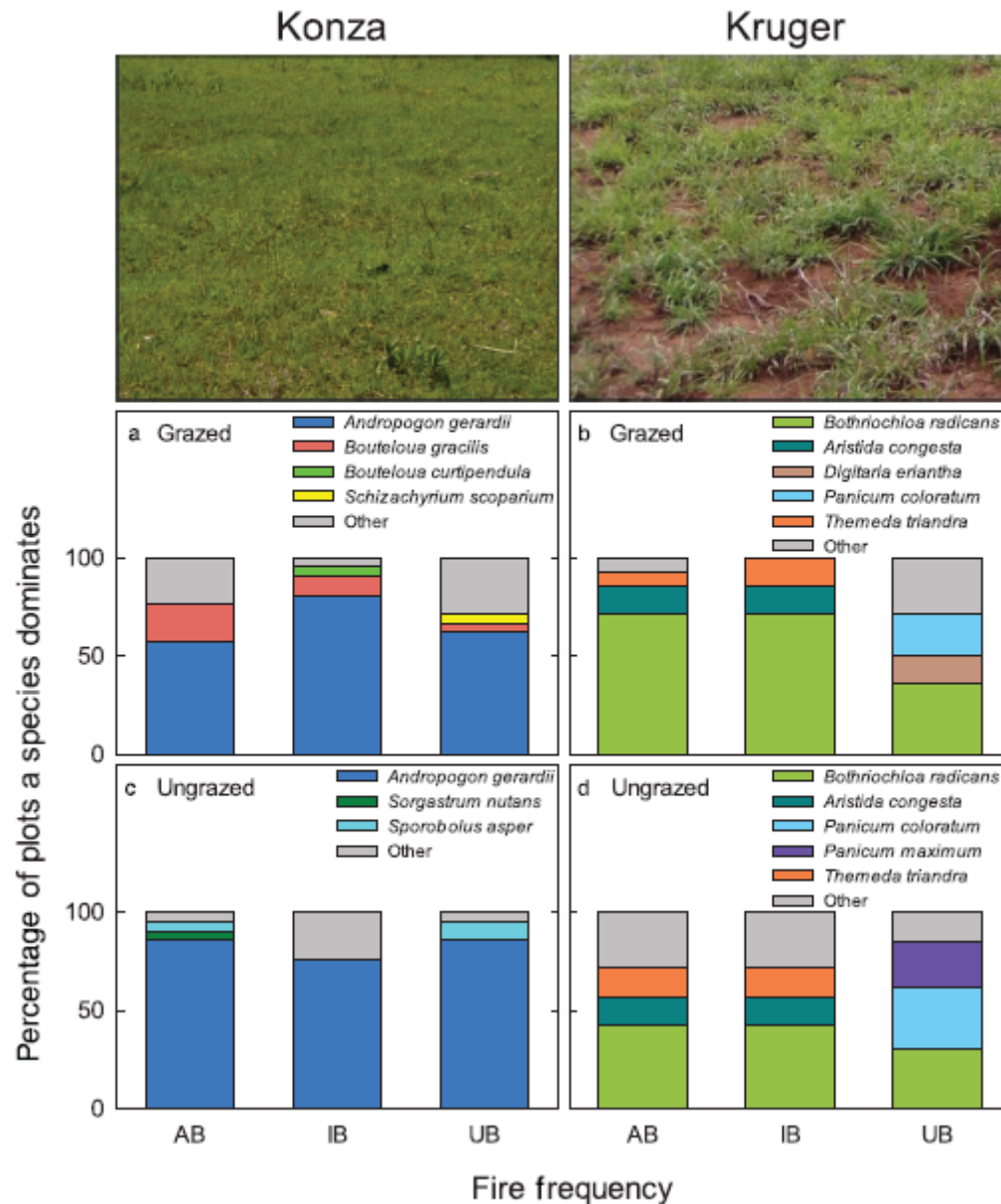


Figure 8. (top) Contrasting growth forms of C₄ grasses at Konza (left) and Kruger (right). The photos illustrate a key difference in traits among the dominant grasses: At Konza, they are rhizomatous (sod-forming) species capable of rapid population growth, whereas at Kruger, they are primarily caespitose (bunchgrass), a growth form less likely to spread rapidly. (bottom) The percentage of plots dominated by the most common grass species in grazed (a, b) and ungrazed (c, d) plots within the three fire-frequency treatments at Konza (left) and Kruger (right). Note that unpalatable grasses such as *Bothriochloa radicans* and *Aristida congesta* are only present at Kruger.

Finally, the role of predation risk as a determinant of habitat selection differs strongly between Konza and Kruger. In Kruger, predators such as lion (*Panthera leo*) and hyena (*Crocuta crocuta*) are common, and leopard (*Panthera pardus*), cheetah (*Acinonyx jubatus*), and wild dog (*Lycaon pictus*) are also present. These predators likely force herbivores to balance food availability and predation risk when selecting habitats. For example, herbivores such as African buffalo, wildebeest, and giraffe exhibited a significant trade-off between food acquisition and minimizing predation risk from lions by foraging in areas with a lower density of woody vegetation, which

often lessens the risk of successful attacks by lions (Burkepile et al. 2013). Predation risk also likely played a role in determining significant day-versus-night dynamics in herbivore habitat selection. For example, impala appeared to use riskier habitats with more diverse forage options during the day (triennial burns and unburned plots) but used less risky habitats at night (annual and triennial burns; Burkepile et al. 2013). In contrast, Konza is a risk-free environment where the historically dominant predators, wolves (*Canis lupus*), are currently absent. Therefore, bison are free to forage without being forced to make trade-offs between safety and food acquisition allowing them to select habitats according to their nutritional needs. Therefore, they appear to spread their foraging more widely and have consistent impacts on plant communities across burn regimes. How the decoupling of herbivores from predation risk (eliminating the “landscape of fear”) affects savanna grassland vegetation dynamics remains an important avenue of research moving forward (Frank 2008, Ford et al. 2014).

The role of diversity, traits and phylogeny of the dominant C₄ grasses

The NA and SA savanna grassland sites are dominated by tall, perennial C₄ grasses. Although the grass communities share no species, there is a high degree of clade overlap, with the Andropogoneae harboring dominant grasses at both sites (Forrestel et al. 2014, 2015). Only a few perennial sod-forming, rhizomatous grasses (primarily *A. gerardii*) dominate (figure 8; similar to other savanna grasslands, Sala et al. 1986, Diamond and Smeins 1988). These grasses are palatable and capable of relatively rapid regrowth after fire because of traits associated with grazing tolerance (Forrestel et al. 2015) and enhanced competitive ability under high light and low nitrogen availability (Forrestel et al. 2014). For example, extensive belowground bud banks and asexual reproduction allow populations of these species to rapidly increase in abundance with fire and grazing (Benson and Hartnett 2006). Although *A. gerardii* decreases in dominance with grazing, it remains common with or without grazing and regardless of fire frequency (figure 8; Knapp et al. 1999). Therefore, how this species responds to fire and grazing is a key determinant of overall plant-community responses.

In contrast, there is much higher diversity of grasses overall in SA savanna grasslands and a greater representation of species within the dominant Andropogoneae clade (Forrestel et al. 2014, 2015). The identity of the dominant grass clade in any particular site in SA is determined primarily by fire frequency (figure 8; Fynn et al. 2004, Eby et al. 2014, Forrestel et al. 2014). With frequent fire in the absence of grazing, Andropogoneae species increase in abundance (Forrestel et al. 2014). However, given that this clade is more diverse in SA, increased abundance of these species contributes to an increase in plant richness with frequent fire that is not observed in the depauperate Andropogoneae clade at Konza (figure 3, bottom; Kirkman et al. 2014). With frequent fire and grazing, unpalatable C₄ grasses, in particular the Andropogoneae species *Bothriochloa radicans* (and to a lesser extent *Aristida congesta*), strongly dominate (figure 8). Whereas in long-term unburned sites, *B. radicans* codominates along with palatable C₄ grasses (*Panicum coloratum*, *Panicum maximum*, *Digitaria eriantha*; figure 8). *B. radicans* is thought to avoid grazing by producing an array of aromatic compounds (van Oudtshoorn 2012). Functional traits of *B. radicans* align more closely with other grazing-tolerant or drought-adapted grass species (e.g., *Bouteloua gracilis*, which dominates unproductive grasslands in NA) than with other Andropogoneae species (Forrestel et al. 2015). Therefore, this unpalatable dominant grass experiences limited grazing, or when it is grazed (in

the early spring), it is more tolerant of grazing than the palatable grasses (Swemmer et al. 2007). This difference in palatability/grazing tolerance becomes particularly important in burned areas that attract high densities of grazers that target grasses (e.g., zebra, wildebeest; figure 7). The combination of high dominance by *B. radicans* and high herbivore abundance results in intense grazing pressures on the palatable grasses in burned sites, leading to the loss of these species (figure 8). In addition, with its dense canopy and potential allelopathic properties (Scrivanti et al. 2011), *B. radicans* may prevent colonization by more palatable grasses (Anderson and Briske 1995, Hussain et al. 1982, Schmidt et al. 2008) and forb species (Koerner and Collins 2014), even in the absence of grazing. The low abundance of palatable grasses in sites dominated by *B. radicans* may further constrain colonization because of propagule limitation. Indeed, palatable grasses increased in abundance with removal of grazing only in unburned sites (figure 8), potentially because these species and their propagules were already present at relatively higher abundances. Taken together, the traits of the dominant grasses at Kruger—ranging from caespitose palatable grasses that are limited in their ability to rapidly expand to the unpalatable *B. radicans* with potential allelopathic properties—appear to be constraining plant-community and ecosystem responses to the exclusion of grazers. Indeed, the longevity of *B. radicans* combined with its resistance to grazing and positive response to fire may allow this species to maintain its dominance indefinitely, regardless of grazing pressures.

Ultimately, it is the differences in the traits of the dominant grasses, particularly those in the Andropogoneae clade, and how these are filtered with respect to the long-term fire regimes at NA versus SA that leads to the divergence in responses in plant-community richness. Despite these differences, there is convergence between sites in the response of plant species richness to dominance, with richness decreasing with increasing dominance irrespective of fire or grazing regime. Therefore, the key mechanism determining responses in community richness, the *degree of dominance*, is shared among sites, and divergent-richness responses are a result of the differential impacts of grazing and fire on dominant grasses in both savanna grasslands. The strongest correlation between richness and dominance is found for annually burned sites (Eby et al. 2014, Koerner et al. 2014), which, in the absence of grazing, increases dominance by Andropogoneae grasses at both sites. This dominance mechanism leads to similar increases in ANPP with frequent fire but a difference in plant-richness responses because of the differences in the diversity of Andropogoneae species between the Konza and Ukulinga sites (Forrestel et al. 2014, Kirkman et al. 2014). In contrast, removal of large herbivores increases dominance by Andropogoneae species over time at Konza, with the magnitude of this increase greater with increasing fire frequency (figure 9). Increases in dominance with removal of herbivores are limited at Kruger, occurring only in sites that are dominated by palatable grasses (e.g., unburned sites with a single grazer, Eby et al. 2014). For those sites dominated by the unpalatable grass *B. radicans*, removal of large herbivores has little impact on dominance (figure 9) or plant species richness. We posit that turnover of the identity of dominant species to those that are more palatable will be required in order for increasing dominance to become an important mechanism determining plant-community response to large herbivore loss in SA.

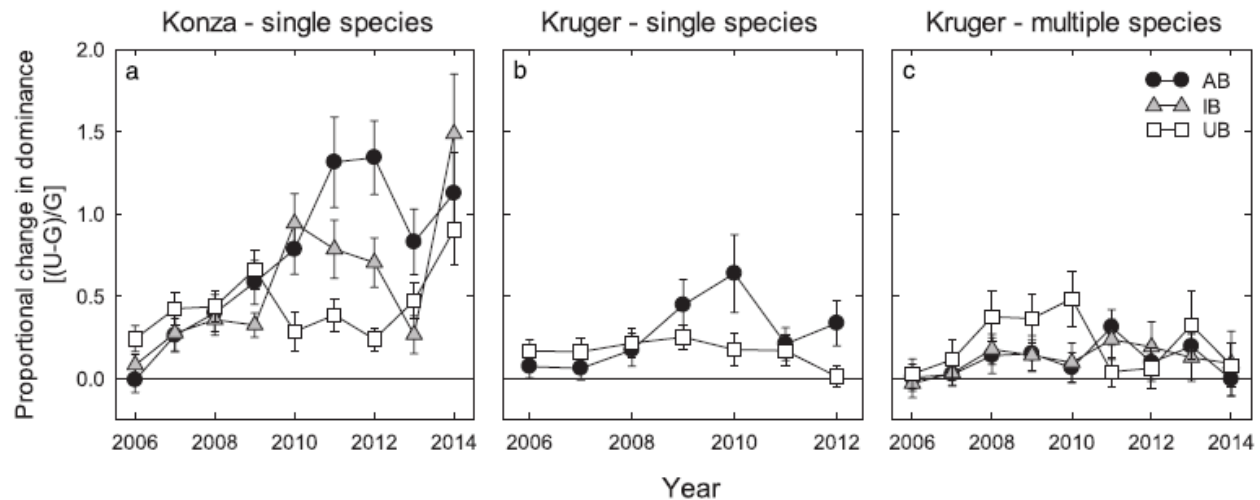


Figure 9. A comparison of the effects of herbivore loss on dominance under different frequency treatments (AB, annual burn, black circles; IB, intermediate burn, gray triangles; UB, unburned, white squares) at Konza (a) and Kruger with a single species of herbivore (b) and multiple herbivores (c). Dominance at the 4-per-m² plot level was measured in grazed and ungrazed plots using the Berger-Parker index (d). The proportional change in dominance was calculated as (ungrazed–grazed)/grazed. A proportional change above zero means that the removal of herbivores increased dominance. Modified from Koerner and colleagues (2014) and Eby and colleagues (2014) with two additions years of data.

Conclusions

With a decade-long comparative experiment, we assessed the extent to which plant-community and ecosystem responses to alterations of fire and grazing were similar in savanna grasslands in NA and SA. Determining whether and when responses are generalizable versus site specific is crucial given the global-scale alterations of fire and grazing regimes due to human activities. By eliminating differences in methodologies as a potential factor leading to divergent responses, we demonstrated that unique plant-community responses do not preclude convergent ecosystem responses to alterations in common drivers. Furthermore, these studies show that these similar and divergent responses at different hierarchical levels can arise from a common mechanism—degree of dominance. Although differences in herbivore diversity, predation risk, and the key traits of the dominant grasses are important to consider, the underlying control of plant species richness by grass dominance at both sites provides a common mechanism explaining community and ecosystem responses to alterations in fire and grazing. Identifying the common mechanisms underpinning community and ecosystem responses is key for generalizing across systems that are thought to be inherently different.

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